

# SYSTEMATICS OF THE *ACALYPHA CALIFORNICA* COMPLEX (EUPHORBIACEAE)

GEOFFREY A. LEVIN

Center for Biodiversity, Illinois Natural History Survey,  
607 East Peabody Drive, Champaign, IL 61820, USA

## ABSTRACT

The *Acalypha californica* complex (Euphorbiaceae) of the southwestern United States and northwestern Mexico has been treated as up to three species, *A. californica* Benth., *A. pringlei* S. Watson, and *A. stokesiae* Pax & K. Hoffm. Most recent authors, however, have recognized only two or one species, without offering supporting evidence. Study of herbarium specimens and population samples from throughout the range of the complex shows that most characters used to segregate the species cannot be used taxonomically because they vary either within individuals or within populations with no geographic pattern. In contrast, the frequency of plants with two distinct lengths of eglandular stem trichomes varies clinally. A different and weaker cline is followed by the number of teeth on the bracts subtending the carpellate flowers. Though in both clines the geographic extremes are different, no gaps in the clines are statistically recognizable. Only a single variable species, *A. californica*, should be recognized.

## RESUMEN

El complejo *Acalypha californica* (Euphorbiaceae) del suroeste de los Estados Unidos y el noroeste de México ha sido tratado como tres especies, *A. californica* Benth., *A. pringlei* S. Watson, y *A. stokesiae* Pax & K. Hoffm. Sin embargo, autores recientes han reconocido solo una o dos especies, sin ofrecer evidencia apoyando este reconocimiento. El estudio de ejemplares del herbario y muestras de las poblaciones de toda la distribución del complejo nos enseña que casi todas las características usadas para segregar las especies no deberían ser usadas taxonómicamente porque hay variación entre individuos o entre poblaciones sin ningún diseño geográfico. Al contraste, la frecuencia de plantas con dos longitudes distintas de las tricomas del tallo eglandular varía gradualmente por toda su distribución. Una gradación diferente y débil se encuentra con el número de dientes en las brácteas que subtenden las flores femeninas. Aunque en las dos gradaciones los extremos geográficos son diferentes, ninguna de las aberturas son reconocidas estadísticamente. Solo una especie variable, *A. californica*, debería ser reconocida.

Most floras (e.g., Wheeler 1942, 1960; Wiggins 1964; Munz 1974; Webster 1993) recognize two shrubby species of *Acalypha* L. (Euphorbiaceae) in the southwestern United States: *A. californica* Benth. in California and *A. pringlei* S. Watson in Arizona. Some authors (Miller 1964; Felger et al. 1992), however, have treated these as a single species, though without presenting supporting evidence. A

third species in this alliance, *A. stokesiae* Pax & K. Hoffm., has also been described, but most authors have overlooked this name. While preparing a treatment of the *Acalypha* of Arizona (Levin in press), I undertook field and herbarium studies to test whether these species, which I will call the *A. californica* complex, are distinct. I present those results here.

*Acalypha californica* was described in 1844 from a specimen collected in Baja California Sur, Mexico (Bentham 1844), and by 1891 was known to range from San Diego County, California, to the Cape Region of Baja California (Watson 1880; Brandegees 1891). Meanwhile, Watson (1885) described *A. pringlei* from a specimen from northwestern Sonora, Mexico. Despite his familiarity with *A. californica*, Watson compared his new species not with this species, but with two from central Mexico. Later, Pax and Hoffmann (1924) reported *A. californica* from Sonora and described *A. stokesiae* (as *stokesii*) from southern California, comparing it (in their key only) with species from South America. The reported range of *A. pringlei* was extended to Arizona by Tidestrom and Kittell (1941) and Wheeler (1942).

Only three publications have dealt with two or more of these names, and each treatment is different. Pax and Hoffmann (1924) recognized three species in the *A. californica* complex and used differences in inflorescence structure to place them in three separate "series," groups taxonomists today probably would equate with sections (cf. Webster 1967). According to their monograph, *A. californica* has strictly axillary inflorescences that are carpellate, staminate, or sometimes androgynous (carpellate below and staminate above); *A. pringlei* has terminal and axillary carpellate inflorescences and axillary staminate (rarely androgynous) inflorescences; and *A. stokesiae* has strictly axillary inflorescences that are either carpellate or androgynous. The androgynous inflorescences of all three species were reported to produce few carpellate flowers. Wiggins (1964) recognized two species, placing *A. stokesiae* in synonymy under *A. californica*. He distinguished *A. californica* from *A. pringlei* based on *A. californica* having (1) the stems with eglandular trichomes of uniform length vs. with some eglandular trichomes at least twice as long as those forming most of the pubescence; (2) the leaf bases cordate vs. truncate or rounded, or rarely cordate; (3) the young foliage often viscid vs. not viscid; and (4) the bracts subtending the carpellate flowers with 15–21 teeth vs. 9–11 teeth. Miller (1964), studying specimens principally from the United States, stated that she could find no differences between *A. californica* and *A. pringlei* but that field work was needed in Mexico; she did not mention *A. stokesiae*. Felger et al. (1992) implicitly recognized only a single species when they reported the shrubby *Acalypha* from southern Arizona as *A. californica*, but they listed no synonyms.

## MATERIALS AND METHODS

Herbarium specimens of *Acalypha californica* and *A. pringlei* were borrowed from A, ARIZ, ASU, B, BM, CAS, DAV, DES, DS, F, GH, MICH, MIN, MO, NY, POM, RSA, SD, UC, UCR, and US; I could locate no specimens labeled *A. stokesiae* even with special requests to herbaria known to have Susan Stokes' collections (Lanjouw and Stafleu 1986). On the 356 specimens that had both new growth and fairly precise locality data, I measured trichome lengths using a Wild M-8 dissecting microscope with an ocular micrometer. I examined new growth near the stem tips to ensure that trichomes had not been lost as the stem weathered or as bark was produced. On the 249 specimens that also had mature bracts subtending carpellate flowers, I counted the number of teeth on three to five bracts oriented so that all teeth were visible. I also studied inflorescence sexuality and position and leaf shape on all herbarium specimens.

To study variation within populations I collected samples from 18 populations in California, Arizona, Baja California, and Sonora; collection data appear in the Appendix. In each population I collected one stem with new growth from each of 20 shrubs scattered through the population. These specimens are deposited at SD. I measured trichomes and counted bract teeth using the same protocol as for the herbarium specimens. Though it seemed impractical to quantify viscidness, while in the field I handled the young foliage in an attempt to subjectively assess how sticky it was.

I preserved some young stems in FAA (formalin-acetic acid-ethanol) from one population each in California, Baja California, and Sonora. To study trichome morphology I cut free-hand cross sections of the preserved stems with a razor blade, mounted the unstained sections on a microscope slide, and examined them with a Nikon Labophot compound microscope.

*Statistical analyses.* I analyzed geographic variation in the frequency of indument types using the  $\chi^2$  test for independence using actual proportions (Zar 1984). Where I found significant differences, I then did multiple comparisons using a Tukey-type test for proportions (Zar 1984). For this test I normalized the proportions using the modified arcsine transformation Zar (1984, formula 14.5) recommended be used when many proportions are large or small, as was the case with these data. I tested for geographic differences in numbers of bract teeth using the Kruskal-Wallis single factor analysis of variance by ranks, followed by non-parametric multiple comparisons using the Tukey test with the ranked data (Zar 1984). Because my sample sizes were large, I used Student's t-test with unequal variances to determine if numbers of bract teeth differed between plants with different indument types. These analyses were carried out using spreadsheet and statistical functions in Quattro Pro for

Windows (Borland International, Inc. 1993). To further test the strength of the geographic patterns observed, I performed a discriminant analysis with cross validation using Systat for Windows (Systat, Inc. 1992).

## RESULTS

*Inflorescence position and sexuality.* Throughout the range of the *A. californica* complex, many plants produce both terminal and axillary inflorescences. Terminal inflorescences are uniformly carpellate, but apparently are not produced consistently by every plant. Axillary inflorescences predominate and may be staminate, carpellate, or androgynous with 1–3 carpellate flowers at the base; all three types frequently are present on a single plant. Occasional plants bear a single carpellate flower at the apex of staminate or androgynous inflorescences.

*Leaf base shape.* The shape of the leaf bases in the *A. californica* complex is quite variable. Even on the same plant they may be cordate, rounded, truncate, or occasionally obtuse. Because the variability within plants made this character of little taxonomic value, I did not try to quantify base shape.

*Foliage viscidness.* I was unable to find any consistent differences in foliage viscidness throughout the geographic range of the *A. californica* complex. This characteristic may be primarily environmentally determined: leaves produced on lush growth under good growing conditions often were viscid whereas those produced under drier or hotter conditions were not.

*Stem trichome morphology.* All plants in the *A. californica* complex produce two types of trichomes on their stems, glandular and eglandular. Glandular trichomes are multiseriate with a stalk about four cells across and several cells long bearing a spherical to oblate multicellular head. These trichomes are yellowish in color and 0.05–0.2 mm (rarely to 0.5 mm) long. Eglandular trichomes are uniseriate. Lengths are quite variable, ranging from 0.1 to 1.2 mm, with the shortest trichomes consisting of as few as two cells and longest of as many as seven cells. Other than cell number, I saw no morphological differences between short and long trichomes.

The lengths of the eglandular stem trichomes on individual plants fell into three basic patterns. In the first pattern, found on 208 (58%) of the 356 herbarium specimens examined, the trichome lengths showed little variation, with the range no more than 0.2 mm; on all but six of these specimens the trichomes were all less than 0.3 mm long. Of the specimens with more variation, most (117, 33% of total specimens) showed the second pattern, bearing short (0.1–0.3 mm long) trichomes mixed with others 2–10 times as long. Only 31 (9%)

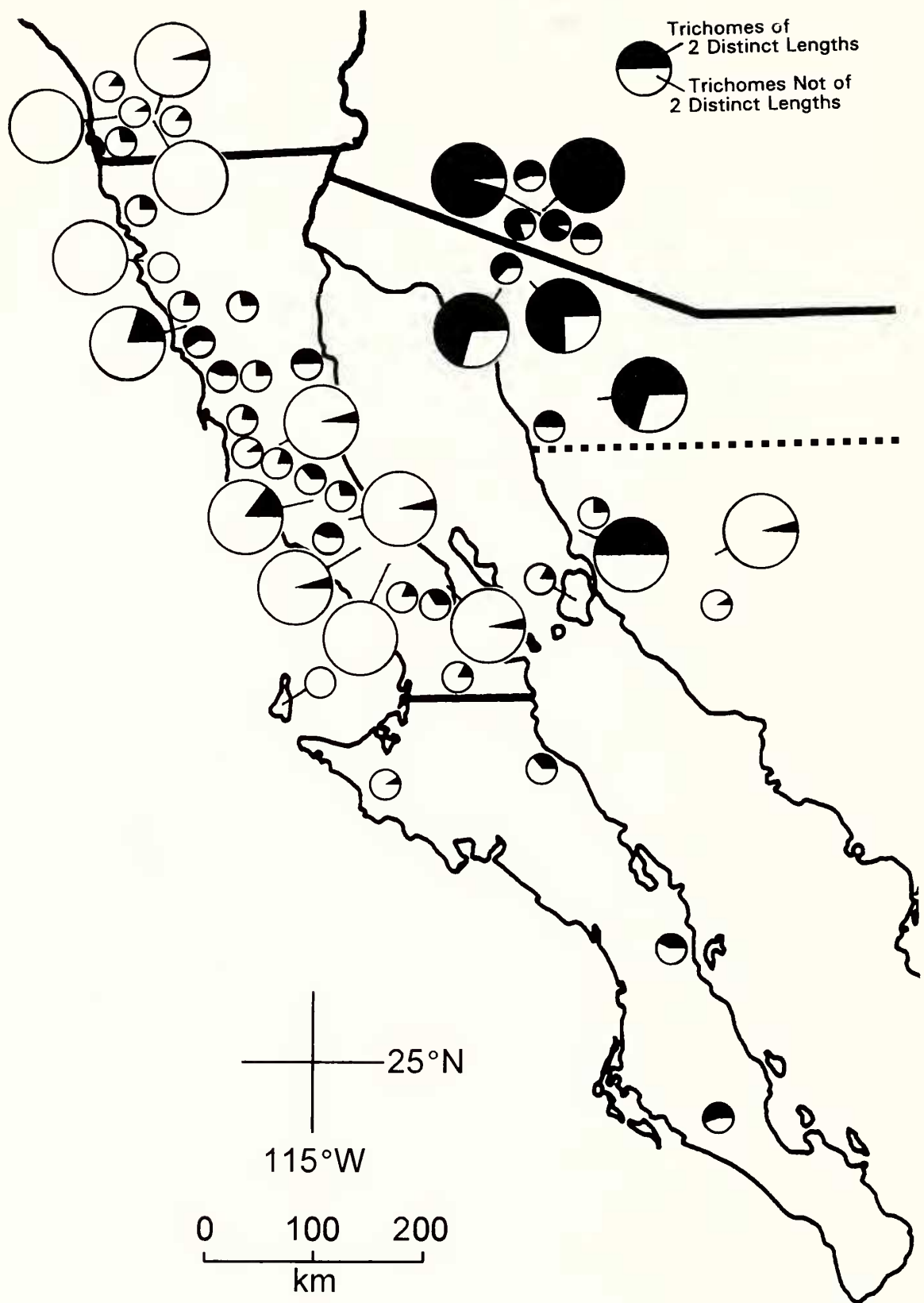


FIG. 1. Southwestern United States and northwestern Mexico showing geographic variation within the *Acalypha californica* complex in the frequency of plants with two distinct lengths of eglandular stem trichomes. Small pie charts are based on herbarium specimens; 7-14 herbarium specimens from the same geographic region were grouped and a pie chart placed at their mean position. Large pie charts summarize population samples of 20 plants each. The dashed line in Sonora represents 30°N latitude.

TABLE 1. REGIONAL VARIATION IN STEM INDUMENT AND BRACT TOOTHING SHOWN BY HERBARIUM SPECIMENS OF THE *ACALYPHA CALIFORNICA* COMPLEX. Sample sizes are shown in parentheses; not all specimens had mature bracts so these sample sizes are smaller. Values followed by the same superscript letter are not statistically different (multiple comparisons using Tukey test with arcsine transformed proportions (stem indument) or ranked data (bract tooting),  $P > 0.05$ ).

Region	Frequency of specimens with two distinct lengths of eglandular stem trichomes	Mean number of bract teeth
California	16.7% (36) <sup>a</sup>	13.24 (19) <sup>ab</sup>
Sonora south of 30°N	16.7% (30) <sup>a</sup>	12.69 (21) <sup>ab</sup>
Baja California	26.4% (178) <sup>ab</sup>	13.69 (127) <sup>a</sup>
Baja California Sur	36.7% (49) <sup>bc</sup>	13.61 (36) <sup>ab</sup>
Sonora north of 30°N	54.5% (22) <sup>cd</sup>	12.68 (14) <sup>b</sup>
Arizona	70.7% (41) <sup>d</sup>	12.62 (32) <sup>b</sup>

specimens had the third pattern, trichomes that varied continuously in length with a range  $>0.2$  mm. The population samples showed the same three patterns, again with very few individuals showing continuous variation. Because the frequencies of continuous variation in trichome length were small and close to statistical expectations, this class had little impact on the statistical analyses that follow; the same test results were obtained recognizing this class or combining it with either of the other two classes. For ease of data presentation and interpretation, I therefore recognized two categories of specimens: those with two distinct lengths of eglandular stem trichomes and those with little or continuous variation in length. This division parallels Wiggins' (1964) distinction between *A. pringlei* and *A. californica*.

In no case did different branches of a single plant show different patterns of eglandular stem trichome lengths. However herbarium specimens from nearby locations often differed, with the frequency of the two classes varying geographically (Fig. 1). To test whether this variation was statistically significant, I divided the specimens into six geographic areas (Table 1): Arizona, Baja California (Norte), Baja California Sur, California, northern Sonora (north of 30°N latitude), and central Sonora (south of 30°). I separated Sonora into these two areas because of Wiggins' (1964) statement that only *A. pringlei* grows in the northern part of the state whereas both *A. californica* and *A. pringlei* grow in the central region. The frequencies were not independent of geography ( $\chi^2 = 42.88$ ,  $df = 5$ ,  $P < 0.001$ ), but formed a cline with the frequency of specimens with two distinct lengths of eglandular stem trichomes being lowest in California and increasing through Baja California, Baja California Sur, northern

TABLE 2. FREQUENCY OF PLANTS WITH TWO DISTINCT LENGTHS OF EGLANDULAR STEM TRICHOMES IN POPULATIONS OF THE *ACALYPHA CALIFORNICA* COMPLEX. Each population is represented by 20 plants. Populations are numbered with my collection numbers; detailed locality information appears in the Appendix. Populations followed by the same superscript letter are not statistically different (multiple comparisons using Tukey test with arcsine transformed proportions,  $P > 0.05$ ).

Locality	Frequency (%)
California: 2152 <sup>a</sup>	0
California: 2192 <sup>a</sup>	0
Baja California: 2130 <sup>a</sup>	0
Baja California: 2141 <sup>a</sup>	0
California: 2150 <sup>ab</sup>	5
Baja California: 2134 <sup>ab</sup>	5
Baja California: 2138 <sup>ab</sup>	5
Baja California: 2140 <sup>ab</sup>	5
Baja California: 2145 <sup>ab</sup>	5
Sonora (south of 30°): 2190 <sup>ab</sup>	5
Baja California: 2137 <sup>ab</sup>	15
Baja California: 2133 <sup>bc</sup>	20
Sonora (south of 30°): 2187 <sup>cd</sup>	50
Sonora (north of 30°): 2173 <sup>d</sup>	70
Sonora (north of 30°): 2191 <sup>d</sup>	70
Sonora (north of 30°): 2156 <sup>de</sup>	75
Arizona: 2154 <sup>ef</sup>	95
Arizona: 2155 <sup>f</sup>	100

Sonora, to Arizona. Adjacent areas in this cline did not differ, whereas more distant areas were significantly different (Table 1). Central Sonora had a lower frequency of specimens with two distinct lengths of eglandular stem trichomes than did northern Sonora, but the frequency did not differ from that found in Baja California and California (Table 1).

Individual plants from the same population also often had different patterns of eglandular stem trichome lengths (Fig. 1, Table 2), and the frequency of plants with two distinct lengths of eglandular stem trichomes was not independent of population ( $\chi^2 = 217$ ,  $df = 17$ ,  $P < 0.001$ ). When the populations were sorted by frequency, they showed a cline generally similar to that shown by the specimens (Table 2). In both Baja California and central Sonora, however, there were significant differences among populations from the same region, indicating that there is considerable local variation within the overall cline, a pattern also shown by the herbarium specimens (Fig. 1) and reflected in the results of the discriminant analysis (see below). In addition, there was less association of populations from central Sonora with those from Baja California and California than there was with the herbarium specimens, perhaps as a consequence of more restricted sampling with the populations (two samples from inland

areas) than with the specimens (30 specimens from a wide geographic area).

*Bract tooth number.* The number of teeth on the bracts subtending the carpellate flowers varied from eight to 21, with lower numbers generally in Arizona and Sonora and higher numbers generally in Baja California and California (Table 1). Herbarium specimens from the six geographic regions differed significantly (Kruskal-Wallis test:  $H = 16.919$ ,  $df = 5$ ,  $P < 0.01$ ). The sequence of geographic regions was different from that shown by the eglandular stem trichome lengths, however, and only the extremes (Arizona and northern Sonora vs. Baja California) differed statistically (Table 1). The number of bract teeth did not differ between specimens in the two trichome classes (Student's  $t = 0.795$ ,  $df = 141$ ,  $P$  [two-tailed] = 0.43), further showing the weak association between bract toothiness and stem trichome characteristics. Too few plants in the population samples bore mature bracts to use these for statistical tests.

*Discriminant analysis.* Another way to evaluate these geographic patterns is through discriminant analysis with cross validation. In this procedure, a portion of the data is used to construct a discriminant function. For cross validation, this function is then used to predict the group assignments of the remaining portion of the original data. The more accurately the predicted assignments reflect actual group membership, the better the data distinguish among the groups. Using the herbarium specimens and data on both trichome type and bract toothiness, I tested two scales of geographic classification. In each case I randomly selected approximately half the specimens for the analysis and used the remaining specimens for cross validation. When the specimens were sorted into the six geographic regions discussed above, 52% of the specimens were assigned to their correct regions during cross validation. However, when the specimens were sorted into the 35 groups represented by the small pie charts in Figure 1, only 8% of the specimens were correctly assigned. Therefore eglandular trichome pattern and bract toothiness separate large regions moderately well, but local regions poorly. Stated differently, there may be statistically significant clines in these characters, but the clines are weak and subject to considerable local variation.

## DISCUSSION

When Pax and Hoffmann (1924) revised *Acalypha*, they examined very little Mexican material (McVaugh 1961), indeed only three specimens in the *A. californica* complex (two of *A. californica*, one of *A. stokesiae*, and none of *A. pringlei*). Study of more material invalidates the supposed differences in inflorescence position and



sexuality that Pax and Hoffmann used to place these species in three different subgeneric groups. This error is symptomatic of the overall weakness of their classification, in which they emphasized mechanical separation of species by key characters, often at the expense of showing taxonomic relationships (Standley and Steyermark 1949).

Among the characteristics that Wiggins (1964) used to distinguish *A. californica* and *A. pringlei*, both leaf shape and herbage viscidness vary widely within and among individual plants. More significant are the differences in eglandular stem trichome lengths and bract tooth number, both of which show clinal variation. Plants from California form one extreme ("*A. californica*") and those from Arizona form the other ("*A. pringlei*"), but plants from intermediate locations bridge the gap. From an ecological standpoint, these differences may reflect adaptation to different selective pressures, as has been shown with some other clines (e.g., Jones 1973; Briggs and Schultz 1990). Trichomes may be important in defense against herbivores (Ågren and Schemske 1993) or in drought tolerance (Ehleringer 1984). They may instead be genetically linked with other characteristics that are adaptive (Ågren and Schemske 1994), which might be the case also with bract tooth number, which has no obvious adaptive function. I have no direct evidence that either of these traits is genetically rather than environmentally controlled, but specimens (*Balls 19566, 18869; Campbell 20504; Gibson 1636; Shultz 4900*) taken from plants grown at the Rancho Santa Ana Botanical Garden in Claremont, CA, do not vary in either trait from each other or from their maternal parent collected in San Diego County, California (*Wolf 9490*).

From a taxonomic standpoint, two conclusions could be drawn from my analysis of these data. First, this complex could consist of two broadly sympatric species that differ morphologically almost exclusively in trichome features, with one species being more common at one end of the distribution and the other species at the other end. Both species would exhibit the same pattern of geographic variation in bract tooth number. Alternatively, there could be a single species with clinal variation in eglandular stem trichome lengths and bract tooth number. I find the second conclusion more plausible, because I think it unlikely both (1) that two sympatric species of wind-pollinated perennial plants would differ in such a trivial characteristic as trichome type and (2) that bract tooth number would show the same geographic pattern in two distinct species. In the absence of evidence to the contrary, I conclude that this complex consists of a single species. The prevalence of variation both within populations and among nearby populations (Fig. 1) argues against recognition even of infraspecific taxa. Instead, I agree with Miller (1964) that the *A. californica* complex should be treated as a single variable species, with the following synonymy:

- Acalypha californica* Benth., Bot. Voy. Sulph. 51. 1844. *Ricinocarpus californicus* (Benth.) Kuntze, Revis Gen. Pl. 2:617. 1891.—TYPE: MEXICO, Lower California [Baja California Sur], Magdalena Bay, hills, October-November 1839, *G. W. Barclay* (lectotype, BM! [photos DS!, NY!, POM!]; isolectotypes K, LE, MIN!, MO!, RSA!, U; lectotype designated here).
- Acalypha pringlei* S. Wats., Proc. Amer. Acad. Arts 20:373. 1885.—TYPE: MEXICO, Sonora, ravines, shore of Gulf of California, 29 March 1884, *C. G. Pringle* (holotype, GH!; isotypes, A!, CAS!, F[2]!, MICH!, NY[2]!, US[3]!).
- Acalypha stokesiae* [as “*stokesii*”] Pax & K. Hoffm., Pflanzenreich IV. 147. xvi. (Heft 85) 138. 1924.—TYPE: USA, California, San Diego Co., San Diego, *S. Stokes* (holotype, B†; no photographs or isotypes found). I have seen no specimens with this name, but there is no other *Acalypha* in San Diego Co. Designating a neotype seems unnecessary.

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#### APPENDIX

Collection data for *Acalypha californica* population samples.

- Levin 2130*: MEXICO, Baja California, Punta Banda, 7 km S of Hwy. 23 along dirt road branching from road to Los Arbolitos, 31°41'N, 116°31'W, 300 m, 14 October 1991.
- Levin 2133*: MEXICO, Baja California, Hwy. 1, 20.8 km SE of San Vicente, 31°10'N, 116°08'W, 200 m, 14 October 1991.
- Levin 2134*: MEXICO, Baja California, Hwy. 1, 20.2 km E of El Rosario, 30°03'N, 115°33'W, 300 m, 15 October 1991.
- Levin 2137*: MEXICO, Baja California, Hwy. 1 just S of Sonora, where wash crosses road, 29°54'N, 114°56'W, 650 m, 15 October 1991.
- Levin 2138*: MEXICO, Baja California, Hwy. 1, ca. 6 km NW of Hotel La Pinta, Cataviña, 29°47'N, 114°48'W, 600 m, 16 October 1991.

- Levin 2140*: MEXICO, Baja California, 17.9 km SE of Hotel La Pinta, Cataviña, 29°39'N, 114°37'W, 715 m, 16 October 1991.
- Levin 2141*: MEXICO, Baja California, Hwy. 1, 13 km SE of Nueva Chapala and 35.7 km NW of turnoff to Bahía de Los Angeles, 29°19'N, 114°21'W, 625 m, 16 October 1991.
- Levin 2145*: MEXICO, Baja California, 6.6 km NW of Bahía de Los Angeles at Arroyo Columpia, 28°59'N, 113°36'W, 180 m, 17 October 1991.
- Levin 2150*: USA, California, San Diego Co., Anza-Borrego Desert State Park, unnamed canyon draining N side of Inner Pasture, crossing Hwy. S-2 just N of June Wash, 32°56'N, 116°16'W, 365–395 m, 8 April 1992.
- Levin 2152*: USA, California, San Diego Co., Anza-Borrego Desert State Park, Indian Gorge 1.5 km W of Hwy. S-2, 32°52'N, 116°13'W, 275 m, 8 April 1992.
- Levin 2154*: USA, Arizona, Pima Co., Organ Pipe Cactus National Monument, Ajo Mountain Drive about 5 km NE of Hwy. 85, near junction of loop, 31°58'N, 112°47'W, 540 m, 12 April 1992.
- Levin 2155*: USA, Arizona, Pima Co., Organ Pipe Cactus National Monument, Estes Canyon, 32°01'N, 112°42'W, 730–755 m, 12 April 1992.
- Levin 2156*: MEXICO, Sonora, Mun. Puerto Peñasco, Hwy. 2, 17.7 km S of Sonoyta near where ridge of Sierra Cubabi approaches road, 31°43'N, 112°51'W, 500 m, 13 April 1992.
- Levin 2173*: MEXICO, Sonora, Mun. Pitiquito, 16 km S of Pitiquito on road to Puerto de la Libertad, 30°32'N, 112°01'W, 350 m, 14 April 1992.
- Levin 2187*: MEXICO, Sonora, Mun. Pitiquito, 101 km NW of Morelos on hwy. to Puerto de la Libertad, ca. 4.5 km SE of turnoff to San Ignacio, 29°36'N, 112°16'W, 200 m, 16 April 1992.
- Levin 2190*: MEXICO, Sonora, Mun. Hermosillo, N of Hermosillo at junction of Hwy. 15 and Hwy. 21, 29°10'N, 110°55'W, 300 m, 17 April 1992.
- Levin 2191*: MEXICO, Sonora, Mun. Puerto Peñasco, Hwy. 8 18.4 km SW of Sonoyta (Hwy. 2), near SW end of Sierra Cipriano, 31°46'N, 113°00'W, 400 m, 17 April 1992.
- Levin 2192*: USA, California, San Diego Co., Poway, W slope of Twin Peaks, E of E end of Monte Vista Rd., 32°59'N, 117°03'W, 200–230 m, 27 May 1992.